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Gibberellic Acid Stimulation of Cucumber Hypocotyl Elongation[1]

Effects on Growth, Turgor, Osmotic Pressure, and Cell Wall Properties

Anne Taylor and Daniel J. Cosgrove*

Department of Biology, The Pennsylvania State University, University Park, Pennsylvania 16802

ABSTRACT

Recently developed techniques have been used to reinvestigate the mechanism by which gibberellic acid (GA_3) stimulates elongation of light-grown cucumber (*Cucumis sativus* L.) seedlings. Osmotic pressure and turgor pressure were slightly reduced in GA_3-treated seedlings, which elongated 3.5 times faster than control seedlings. This indicated that GA_3 enhancement of growth was not controlled by changes in the osmotic properties of the tissues. Stress/strain (Instron) analysis revealed that plastic extension of the cell walls of GA_3-treated seedlings increased by up to 35% above the control values. Stress-relaxation measurements on frozen-thawed tissue showed that T_0, the minimum relaxation time, was reduced following application of GA_3. *In vivo* wall relaxation (measured by the pressure block technique) showed that the wall yield coefficient was increased, and the yield threshold was slightly reduced. Thus GA_3 affected both the mechanical (viscoelastic) and biochemical (chemorheological) properties of the cell walls of light-grown cucumber. The previous hypothesis, that GA_3 stimulates cucumber hypocotyl growth by increasing osmotic pressure and cell turgor, is contradicted by our results.

GA_3 can reverse the inhibition of stem elongation caused by light in many plant species (1, 12, 17, 18, 21, 23, 24). The mechanism by which GA_3 enhances the rate of elongation has been investigated by several groups, many of whom have concluded that GA_3 acts on cell wall mechanical properties to increase growth (2, 13, 15, 18, 20).

Cucumber is an often-cited exception to this general trend, in that GA_3 is thought to stimulate hypocotyl elongation by causing increases in cell turgor pressure and osmotic pressure. This hypothesis, however, is based on meager direct evidence. Rather, it is indirectly supported by studies which found little effect of GA_3 on the mechanical properties of growing walls (5, 14), and it assumes that wall growth properties are well correlated with wall mechanical properties (4). This assumption, however, is sometimes invalid. For example, a recent study (8) showed that blue light retarded stem elongation in cucumber by inhibiting wall yielding, yet it had negligible effect on wall mechanical properties as measured by the Instron technique. This result led us to suspect that mechanical assays of wall extension may not be sensitive indicators of the wall properties that govern cell expansion in cucumber.

Therefore, this study was undertaken to reexamine the mechanism by which GA stimulated elongation in light-grown cucumber. Osmotic and turgor pressures were measured directly, and *in vivo* wall relaxation properties were assessed in living tissue using the pressure block technique. We also assessed wall mechanical properties in frozen-thawed tissue by stress-relaxation and Instron analyses.

MATERIALS AND METHODS

Plant Material

Seedlings of *Cucumis sativus* L. (var Burpee's Pickler, from A. W. Burpee, Westminster, PA) were grown in darkness for 24 h at 26 to 28°C in vials (72 × 22 mm) of vermiculite soaked with 25% Hoagland solution which contained 5 mM KNO_3, 5 mM $Ca(NO_3)_2$, 2 mM $MgSO_4$, 1 mM KH_2PO_4 (11). After 24 h, the vials were placed in continuous light for 48 h. GA_3 (100 μg; Calbiochem, La Jolla, CA) was then applied in a 10-μL drop of 95% ethanol to the cotyledons or apical bud (5). Control seedlings were treated with a 10-μL drop of ethanol. There was no visual sign of cell damage from the ethanol application. All experiments were carried out at 26 to 28°C.

Light Treatments

Three light treatments were used during this study: (a) overhead white light (W^2), fluence rate at plant height = 108 μmol m^{-2} s^{-1} (51-W Sylvania cool white fluorescent tubes); (b) bilateral blue light (B), fluence rate = 20 μmol m^{-2} s^{-1} (150-W General Electric dichro-color flood lamps, filtered through 5 cm of distilled water, one layer of Rohm and Haas blue Plexiglas No. 2424, and one layer of blue celluloid No. 1654 [Mazzuchelli, Castiglione Olona, Varesse, Italy]); and (c) unilateral red light (R), fluence rate = 150 μmol m^{-2} s^{-1} (150-W flood lamp, filtered through 5 cm of distilled water, one layer of Roscolene amber acetate No. 813 [Rosco, Port Chester, NY], one red CBS 650 plastic filter [Carolina Biolog-

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[2] Abbreviations: W, white light; B, blue light; R, red light; RGR, relative growth rate; PEx, plastic extension; EEx, elastic extension; P_i, initial chamber pressure to stop growth; P, turgor pressure; ϵ, volumetric elastic modulus; Y, yield threshold; ϕ, wall yield coefficient.

ical Supply Co., Burlington, NC], and two layers of red cellophane, No. 3153 [Dennison Manufacturing Co., Maynard, MA]). Light was measured with a quantum sensor and LI-1000 datalogger (LiCor, Lincoln, NE).

Hypocotyl lengths were measured by ruler at 24-h intervals, beginning 72 h after the seeds were sown, when GA_3 and ethanol were first applied. In these experiments, GA_3/ethanol applications were made at 24-h intervals.

Time-Lapse Zonal Growth Analysis

Three-day-old seedlings (approximately 24-mm tall) were divided into four zones by applying fine horizontal marks to the hypocotyl with an eyebrow hair coated with black oil-based paint (Speedball, Hunt Manufacturing Co., Statesville, NC). The zones were numbered sequentially from one (apical zone) to four (basal zone). GA_3 or ethanol was then applied to the seedlings, and photographs were taken at hourly intervals for 24 h. Displacement of the marks was analyzed with a digitizing tablet, microcomputer and custom software.

Turgor Pressure and Osmotic Pressure

Turgor and osmotic pressure were measured in the region of the hypocotyl lying 8 to 15 mm below the base of the cotyledons. This region (zone 2) was found to show the largest growth response to GA_3 when compared with ethanol-treated seedlings. Turgor pressure was measured using the pressure probe technique (6, 9). Osmotic pressure was measured with a vapor pressure osmometer (model 5500, Wescor, Logan, UT) using cell sap expressed from the region of the hypocotyl described above. Osmotic pressure was calculated by dividing osmolality by 41 mOsmol kg^{-1} bar^{-1}.

Mechanical Analysis of Walls

Seedlings were harvested 7 h after GA_3 application (when the maximum growth response to GA_3 was elicited) and immediately frozen at −20°C. A 10- to 12-mm section was excised from zone 2 of the hypocotyl, thawed, and then pressed slowly between two glass slides in order to remove excess water, after which the segment was mounted between two clamps of a custom-made stress/strain analyzer (10), leaving a 5-mm section between the clamps. For stress relaxation experiments, the section was extended at a rate of 170 mm min^{-1} until a maximum stress of 25 g was applied. The subsequent decrease in force was recorded over a 5-min period by a microcomputer, with a minimum sampling interval of 2 ms gradually increasing to 2 s. The first approximation of the relaxation spectrum was computed by taking the derivative of the force with respect to log (time in s) and plotting against log (time in s) (25). Programs for these measurements were written in the Asyst language (Asyst Software Technology, Rochester, NY).

For Instron (stress/strain) analysis, the section was extended in two cycles at 3 mm min^{-1}, until a limiting load value of 30 g was reached (3). A second order polynomial was used to fit the resulting curves, from which values for total, elastic and plastic extensibilities were obtained (10).

Pressure Block Experiments

GA_3- or ethanol-treated seedlings (with hypocotyls 25 to 30 mm in length) were sealed into the pressure block apparatus (7, 8) and left to equilibrate for 1 to 2 h, while elongation of zone 2 (approximately 7 mm in length) was monitored with a position transducer inside the chamber. Compressed air was then released into the pressure chamber at a rate just sufficient to prevent further hypocotyl elongation. As wall relaxation proceeded, greater pressure was needed to maintain zero growth rate.

RESULTS

Effect of GA_3 on Cucumber Hypocotyl Elongation

Initial experiments were carried out to determine the type of light inhibition which could be most completely reversed by treatment with GA_3. Seedlings were grown in W, R, or B light, and on day 3 were treated with GA_3, ethanol, or returned to darkness. GA_3 was most effective in reversing the inhibition in R, and least effective in B and W (Fig. 1). This confirms previous work with pea (24) and cucumber (14) seedlings. All further experiments used seedlings grown in continuous R from 24 h after sowing.

Figure 2 shows that the rate of elongation of GA_3-treated seedlings gradually increased from 0 to 12 h after treatment, following which the growth rate declined. By comparison, the elongation rate of the control seedlings was fairly constant throughout the time period of the experiment.

To find the time and region of the hypocotyl where GA_3 had the greatest effect on growth, time-lapse zonal growth analysis was carried out. Marking experiments revealed that the relative response to applied GA_3 differs along the length of the hypocotyl. Figure 3 shows that the RGR of GA_3-treated seedlings was higher than that of the controls in each of the four marked zones at each time interval. The region of the hypocotyl designated 'zone 2' was found to show the largest and most consistent response to applied GA_3, with RGRs up to 3.5 times those of the controls. The remainder of the experiments described in this paper measure the effects of GA_3 or ethanol on zone 2 of the hypocotyl, between 6 to 12 h after treatment, when the largest difference in RGRs was recorded.

Osmotic and Turgor Pressure

Direct measurement of the osmotic pressure of cell sap expressed from zone 2 of the hypocotyl revealed a small decrease (4%) in GA_3-treated seedlings compared to the controls (Table I). Similarly, pressure probe measurements of cells within the same region of the hypocotyl showed that there was a small (6%) reduction in turgor pressure following GA_3 application, compared to the controls (Table I). These results contradict the hypothesis that GA_3 increases elongation by increasing turgor or osmotic pressure.

Stress Relaxation and Instron Analysis

These two methods were used to assess the extent to which GA_3 altered wall mechanical properties. Stress relaxations of

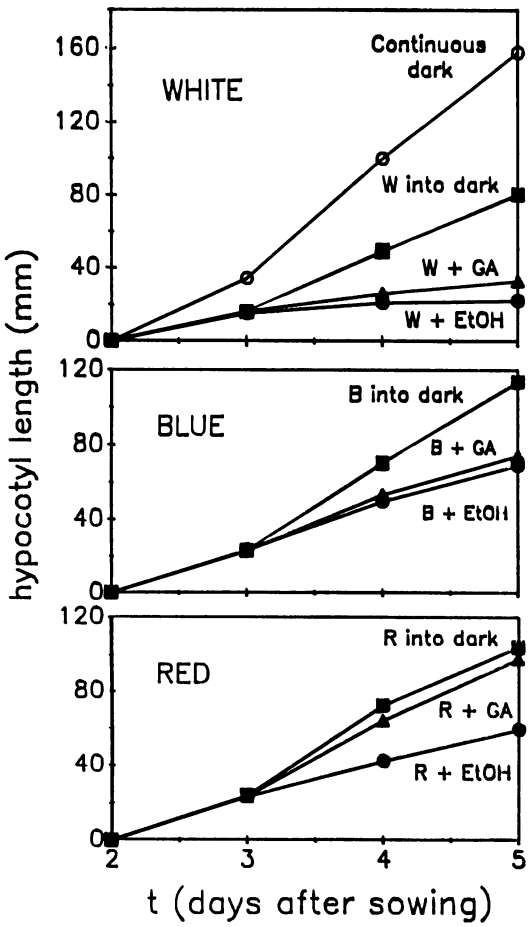

Figure 1. Effects of GA_3 on hypocotyl length of cucumber seedlings grown under different light regimes. One group of seedlings was kept in darkness throughout the experiment. The remainder were grown for 24 h in darkness at 26 to 28°C before exposure to W, B, or R light. After a further 48 h, (*arrowed*), one-third of the seedlings in each light treatment was returned to darkness, 100 μg of GA_3 were applied to another third, and the remainder were treated with ethanol (EtOH) to act as controls (n = 15 to 30 per treatment, SES were typically 10–20%) (■——■, returned to darkness; ▲——▲, GA_3; ●——●, ethanol).

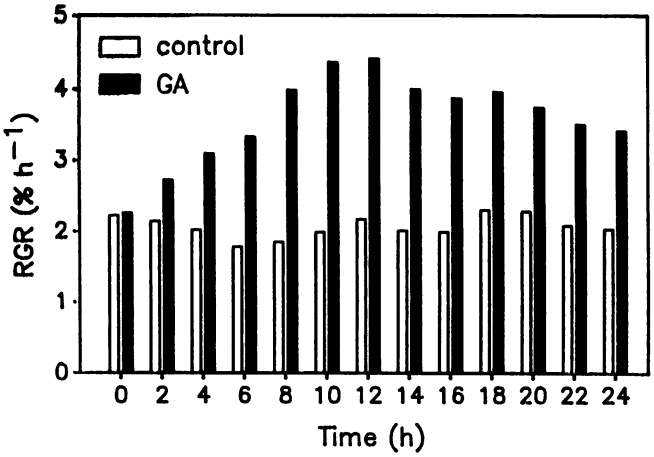

Figure 2. Time course for GA_3 stimulation of relative growth rate of cucumber hypocotyls (whole length) grown in continuous R after 48 h of darkness. At 0 h, the seedlings were 3 d old (n = 13 per treatment, SES were typically 15–20%).

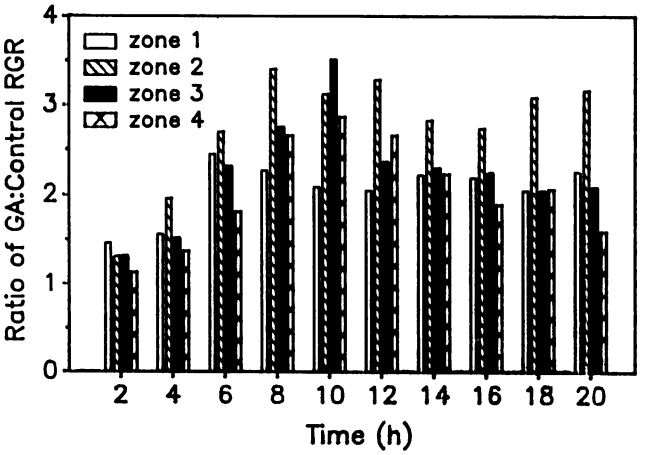

Figure 3. Ratio of the RGRs of 3 d old cucumber seedlings marked into four zones, comparing GA_3-treated seedlings with controls. Zone 1 is the apical region, zone 4 is the basal region. For example, *1* on the *y* axis represents identical growth rates in both treatments; *2* represents a doubling in the RGR of the GA_3-treated seedlings compared with the controls (n = 13 per treatment, SES were typically 15–20%).

individual wall specimens were quite reproducible, but were not 'box-shaped distributions' as reported by Masuda and coworkers (19, 25). Rather, they exhibited at least one broad maximum and two minima in relaxation rates (Fig. 4). The principal effect of GA_3 was a slight shift in relaxation toward shorter times. This corresponds with a decrease in the minimum relaxation time (T_0), but the usual linear-fit technique used to estimate T_0 (19, 25) is fraught with difficulties when the relaxation spectrum is not box-shaped. Instead, we estimated T_0 as the time when the relaxation spectrum reached halfway between minimum and maximum values (Fig. 4). GA_3 decreased this value from 33 ± 0.8 ms to 26 ± 0.6 ms (mean ± SE of 38 samples). The shift in the spectra with GA_3 can be interpreted as an increase in the ability of wall polymers to slip past one another, perhaps due to a reduction in the molecular weight distribution of wall polymers, or a reduction in their entanglements. However, the significance of this change for growth is difficult to evaluate.

Table I. *Osmotic Pressure and Turgor Pressure of Cucumber Hypocotyls 7 h after Treatment with Ethanol or GA_3*

Standard error and sample number are in parentheses. There were significant differences between treatments at the 5% level in both osmotic pressure and turgor pressure, as calculated by ANOVA tests.

Parameter	Ethanol	GA_3
Osmotic pressure (bar)	4.5 (0.05; 39)	4.3 (0.06; 40)
Turgor pressure (bar)	3.3 (0.07; 10)	3.1 (0.04; 10)

Stress/strain (Instron) analysis of the cell walls revealed that the plastic and elastic components of extension were both increased by GA_3, although plastic extension (PEx) was more

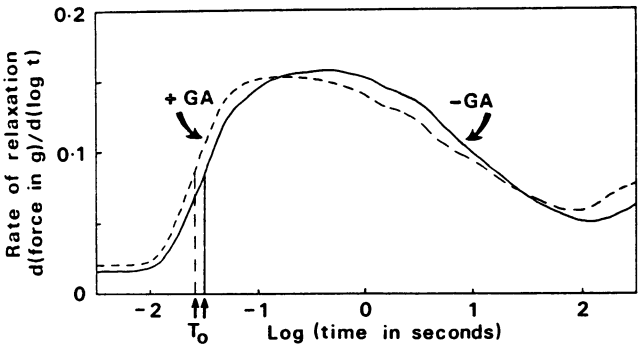

Figure 4. Stress-relaxation spectra for cucumber seedlings treated with GA_3 (- - -) or ethanol (——). The y-axis represents the rate of relaxation in units of d (force in g)/ d(log t). T_0 was estimated as the time when the halfway point between the maximum and minimum rate of relaxation was reached. Each curve is the average of 38 seedlings.

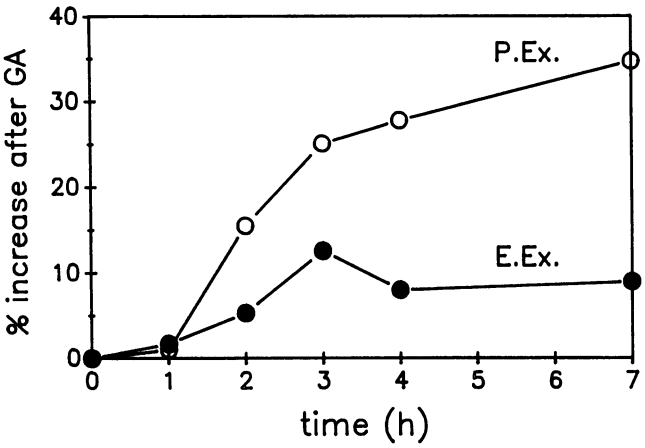

Figure 5. Time course for the effects of GA_3 on plastic and elastic extension of the cell walls of R-grown cucumber hypocotyls, as measured by stress/strain (Instron) analysis. GA_3 or ethanol was applied at 0 h. Significance levels (by ANOVA) were as follows: 5% level: PEx after 2 h, EEx after 4 and 7 h; 1% level: PEx after 3 and 4 h, EEx after 3 h; 0.1% level: PEx after 7 h (n = 20 to 40 per data point).

strongly affected than elastic extension (EEx). A time course for the response showed a significant increase in PEx above the control levels within 2 h of GA_3 application (Fig. 5), when the RGR of zone 2 of GA_3-treated seedlings had increased by 30% (Fig. 3, zone 2). A plot of percent change in PEx against percent change in RGR shows a curvilinear relationship (Fig. 6), unlike the linear relationship reported for IAA-treated oats (3) and maize (16).

Pressure Block Experiments

Figure 7 shows an example of a pressure-block relaxation. In these experiments, the GA_3 treatment was less effective in stimulating growth, evidently because the GA_3 plants were more sensitive to the handling and chamber-sealing procedures than were the controls. Thus, GA_3 caused only a 73% increase in RGR (Table II). Also, some difficulties were experienced during the pressure block experiments, particularly later in the time course, due to apparent oscillations in relaxation (note oscillations in Fig. 7). These might have been artefacts due to nutations.

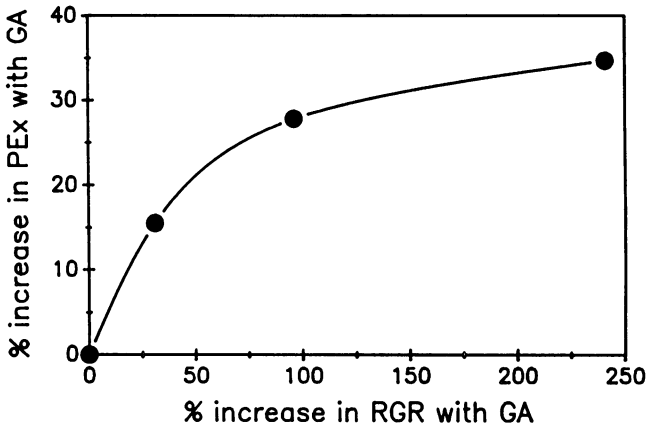

Figure 6. Relationship between RGR and PEx of GA_3- *versus* ethanol-treated cucumber hypocotyls.

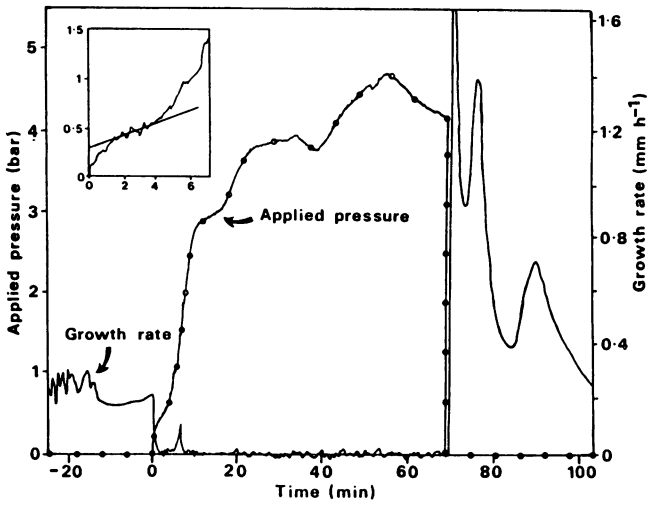

Figure 7. Tracing of the *in vivo* stress-relaxation response of a 3-d-old R-grown cucumber seedling, as measured by the pressure-block technique. The section under analysis was zone 2, which was approximately 7 mm in length at the start of the experiment. Note the immediate fall in growth rate when pressurization of the chamber began. (●—●—●, pressure; ——, growth) *Inset*: the early kinetics of relaxation. Extrapolation of the slope at 2.5 min to the y axis at 0 min provides an estimation of P_i, the initial pressure required to stop growth.

As indicated in Table II, the major effect of GA_3 was on the initial rate of relaxation, which nearly doubled upon GA_3 treatment. In theory (6) this rate is given by $\phi\epsilon$ $(P - Y)$, and so may be used to estimate ϕ (wall yield coefficient) if the other values are known. The value of $(P - Y)$ was increased only slightly (11%) by GA_3 (Table II). It was not feasible to obtain a value for ϵ, the volumetric elastic modulus, because of complications from relaxation of the growing tissue. However, based on the 10% increase in Instron elastic extensibility (Fig. 5), we estimate that ϵ would be decreased slightly (by about 10%) after GA_3 treatment, and thus should effectively cancel out the small increase in $(P - Y)$. By this reasoning,

Table II. *Effects of GA_3 on Pressure-Block Stress Relaxation Parameters*

All measurements were made on 3-d-old R-grown cucumber hypocotyls. Growth rate was measured immediately before pressurization of the chamber began. The initial relaxation rate was obtained by calculating dP/dt from 90 to 210 s after pressurization began (Fig. 7). P_i, the initial pressure required to stop growth, was obtained by taking the point where the slope for initial relaxation rate bisects the y axis at 0 h. An estimate of $(P-Y)$ was obtained by subtracting P_i from the maximum pressure recorded during the first 60 min of the experiment. Y was calculated using the values for (P−Y), and P (Table I). Standard errors are in parentheses.

Parameter	Ethanol (n = 17)	GA_3 (n = 19)	Percent Change after GA_3	Significance Level
Growth rate (% h^{-1})	1.5 (0.24)	2.6 (0.37)	73↑	—*
Initial relaxation rate (bar h^{-1})	3.9 (0.82)	7.4 (1.22)	90↑	—*
P_i (bar)	0.2 (0.03)	0.4 (0.13)	100↑	NS
Maximum P in first 60 min (bar)	3.0 (0.38)	3.5 (0.30)	17↑	NS
$(P-Y)$ bar	2.8 (0.37)	3.1 (0.25)	11↑	NS
Y (bar)	0.5	0.1		

* Significance at 0.05.

we conclude that GA_3 has its primary significant effect on the wall yield coefficient, ϕ.

DISCUSSION

GA_3 increases the elongation of R-grown cucumber hypocotyls, but has little effect on seedlings grown in B or W light. Prior work with cucumber seedlings had attributed the GA_3 stimulation of growth to an increase in cell osmotic pressure (5, 14). However, we found that GA_3 caused a slight reduction in osmotic and turgor pressure of R-grown cucumber hypocotyls. This supports previous work with dwarf watermelon (26) and dark-grown peas (10). Likewise, Stuart and Jones (22) found poor correlation between osmotic pressure and GA_3-induced changes in growth rate in lettuce seedlings.

In previous work (5, 14) the mechanical extension and relaxation properties of light-grown cucumber hypocotyl sections were reported to be unaffected by GA_3 treatment. However, in the stress-relaxation experiments, T_0 was measured only 2 h after GA_3 was applied, and it has been suggested that a longer incubation may be necessary for GA_3 to affect T_0 values (14), as had previously been found for lettuce hypocotyls (15).

In the experiments reported in this paper, both Instron and stress/strain analysis were employed and both gave results which indicated that the cell wall mechanical properties of R-grown cucumbers were altered by GA_3. T_0 was reduced by 20% 7 h after GA_3 was applied. In addition, Instron analysis showed that mechanical extensibility of the cell wall tissue was increased following GA_3 application, with the major increase being in the plastic component (35% after 7 h), although a smaller effect was also found in the elastic component (8% increase after 7 h).

The interpretation of these changes in wall viscoelasticity remains problematic. As pointed out by Katsumi and Kazama (14), changes in cell wall mechanical properties due to GA_3 may be a result rather than a cause of the enhanced growth rate. In our experiments, PEx was significantly increased within 2 h after GA_3 was applied, when the RGR of the same region of the hypocotyl was 30% above the controls. There was a curvilinear relationship between the changes in PEx and RGR (Fig. 6), such that increases in PEx diminished at the higher growth rates. It should be noted that this curve is based on a dynamically changing system, not one in steady state. Thus, we cannot claim that the apparent relationship between PEx and RGR is valid for steady-state growth. Our results indicate that the changes in cell wall viscoelasticity induced by GA_3 are closely linked temporally to the increases in RGR and support previous work with oats (2) and peas (20). These results, however, do not let us conclude that the change in growth rate is the result of the change in PEx, since there is no established fundamental relationship between the two. More likely, the change in PEx (and in T_0) reflects a change in wall structure indirectly associated with the biochemical mechanism of GA_3-stimulated wall yielding.

Why is there a discrepancy between the results reported here and those of Cleland *et al.* (5)? Close examination of their data reveals that there may not be a discrepancy. Their data show that 24 h after GA_3 treatment, the mean RGR was approximately 2.4 times the control value, while PEx was increased by 45%. These results are in agreement with those reported in the current paper. However, during the next 24-h period, the mean RGR of GA_3-treated seedlings remained high, whereas PEx was almost identical to the control values. This may be due to the fact that the RGR represents a mean value for the preceding 24-h period, whereas the values for PEx represent only the current status of the tissue at the time when it was killed (16), or at most measure the average PEx over the previous 60 to 90 min (4). As the mean RGR for the third 24-h period was only marginally higher than that of the controls, the PEx after 48 h may reflect the low RGR at that time. This indicates that the growth rate should be closely monitored at the time when wall viscoelastic properties are measured to ensure accuracy both in the results and in their interpretation.

Recent pressure-block studies from this laboratory have concluded that wall loosening and expansion in pea and cucumber stems has the character of a chemorheological process (8, 10). That is, the wall behaves like a stressed, cross-linked structure that extends principally as a result of biochemical breakage or transfer of load-bearing bonds. While viscoelastic shearing of wall polymers inevitably results from such bond alteration, it does not appear to be rate-limiting for cell enlargement. This would explain why blue-light treatment was found to reduce cell expansion and *in vivo* wall relaxation, yet had only a negligible effect on wall viscoelasticity (8). One of the advantages of the pressure-block method is that it can detect and quantify a chemorheological process that induces wall loosening and relaxation without altering wall viscoelasticity.

In our experiments with R-grown cucumber seedlings, we used the pressure-block technique to measure the growth properties of the wall in terms of the yield threshold (Y) and the wall yield coefficient (ϕ). The yield threshold was reduced slightly by GA_3 treatment (Table II). This reduction in Y would contribute slightly to the increase in growth rate by causing a small increase in $(P - Y)$. In comparison, treatment of dark-grown peas with a GA_3-synthesis inhibitor retarded elongation via a large change in Y, which was reversible upon GA_3 application (10). Although we did not calculate a value for the wall yield coefficient (ϕ), the doubling of the initial rate of relaxation (Table II) indicates that GA_3 treatment caused a substantial increase in ϕ. The changes in wall viscoelasticity noted above may have contributed to this faster relaxation rate (though we have no direct evidence to support this), but because the change in wall viscoelasticity was small relative to the change in wall relaxation rate, we conclude that the major effect of GA_3 was a stimulation of the rate of bond breakage or transfer, with viscoelastic changes in the wall playing a minor role, if any.

To summarize, our experiments have shown that GA_3 does not increase elongation of R-grown cucumber seedlings by increasing the osmotic or turgor pressure of the growing zones. Rather, GA_3 accelerates the biochemical process(es) which cause wall relaxation.

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